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The silicious skeleton of tracheids and fibers*

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(WITH FIVE TEXT FIGURES)

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I. INTRODUCTION AND DISCUSSION OF PROBLEM

It is a remarkable fact that when the water-saturated secondary xylem of the stem is allowed to dry, it shrinks considerably in both radial and tangential diameters but only slightly in length. Conversely, when the dry secondary xylem imbibes water it swells mainly in its radial and tangential dimensions but remains nearly constant in length. The swelling and shrinking of the xylem, therefore, takes place mainly at right angles to the axis of growth. Relative stability of length during the imbibition or evaporation of water is a strongly marked physical property of the xylem in either the living or dead tissues of all woody plants; and the bast, in all cases examined by the writer, has been found to exhibit essentially the same properties of swelling and shrinking as the xylem.

The amount of swelling of the xylem of a large number of species has previously been determined by careful measurements without, however, arriving at a satisfactory explanation of the phenomena observed. The details of anatomy of these tissues have not hitherto made it apparent why one dimension should

* Contribution from the Osborn Botanical Laboratory.

vary independently of another. Nothing in the relative size, shape, or arrangement of the cells would bring about a result of this kind.

In a strand of bast, for example, it is difficult to conceive of any change in the dimensions of the tissue as a whole which would not involve a corresponding change in the dimensions of each component fiber, and this statement would apply equally to the xylem. Hence it is apparent that the basis for an explanation of the phenomena of swelling and shrinking in these mechanical tissues must, in its last analysis, lie, not in the structure of the tissue as composed of cells, but in the structure of the membrane as a part of the cell.

During the years 1917-1920, the writer devoted a portion of the time to a study of the minute structure of the thickened membranes which characterize the mechanical tissues of the stem, and in the course of this work the probable explanation of the phenomena just described became apparent. It was found that longitudinal tracts in the secondary thickening of the wall in the fibers and tracheids of the wood and in the fibers of the bast are more highly mineralized than the material of which the rest of the wall is composed. These mineralized tracts or rods, in which silicious material appears always to be present, run longitudinally from one end of the fiber to the other and constitute a skeleton-like structure (see FIG. 3) which, there is every reason to believe, must have a direct effect upon the physical and mechanical properties of the fiber or tracheid in the walls of which it is imbedded. In contrast to the other parts of the wall substance, these silicious rods imbibe little or no water and hence would neither swell nor shrink with such variation in the amount of imbibition water as may take place in the hygroscopic colloidal material in which they are imbedded, as in a matrix. The matrix, on the other hand, absorbs water freely, so that the dry lignified walls, according to Pfeffer,* may take up as much as 51 per cent of their weight in water. Presumably the colloidal material tends to swell equally in its different axes during imbibition; but the mechanics of movement permitted by the silicious skeleton in relation

* Pfeffer, W. The physiology of plants. English translation. Oxford. Vol. 1, p. 209.

to the colloidal matrix is, to all appearance, such as would almost inhibit any tendency of the fiber or tracheid to swell or shrink longitudinally. Since, however, the rods of the skeleton are not generally connected laterally and would therefore be free to move apart or approach more closely to one another, they would allow the matrix in the spaces between to swell or shrink along any of the transverse diameters of the fibers.

These details in the structure of the cell-wall make it clear that the shrinking or swelling of the xylem or bast would not materially change the longitudinal dimensions of these tissues. Hence the fiber-walls of living tissues, as soon as the silicious skeletons are formed, may function in the diffusion and transport of liquid solutions or may swell or shrink in diameter with the increase or decrease of imbibition water, with the fluctuations of turgor in the cells, or with the changes of sap pressure in the conducting elements; at the same time they may offer the undiminished resistance to longitudinal tension or compression necessary for the mechanical support of the stem. Except for decay, the changes which take place with the death of the cell—in the haulms of rye and other grasses after the ripening of the seed or in the xylem of the tree after one or more years—do not materially affect the structural or physical properties of these tissues.

The writer is indebted to Professors A. W. Evans, G. E. Nichols, and other members of the Department of Botany for material and for many valued suggestions and criticisms throughout the investigation; to Professor H. N. Whitford and other members of the School of Forestry for material of *Tecoma* and other woody plants; and to Professors A. J. Hill of the Department of Chemistry and W. E. Ford of the Department of Mineralogy, to whom portions of the work have been submitted for criticism.

II. HISTOLOGICAL ELEMENTS OF TRACHEIDS AND FIBERS

In the course of the investigation the secondary xylem and, in some cases, the bast of approximately five hundred species were examined by the writer, with the result that the structure of the fiber wall in all was found to be essentially the same. Of

the various species examined, the wood fibers of lapachol-forming* species of *Tecoma* seem as favorable as any for the observation of those details with which this paper is chiefly concerned, and all references to this genus have special application to those species in the vessels of which the sulphur-yellow, monoclinic crystals of lapachol are found.

I. MIDDLE LAMELLA AND PRIMARY THICKENING

In an unstained cross-section of the xylem of *Tecoma* mounted in glycerine, it is observed that the middle lamella and primary thickening of the fiber (FIG. 1, *A*) are highly refractive and not

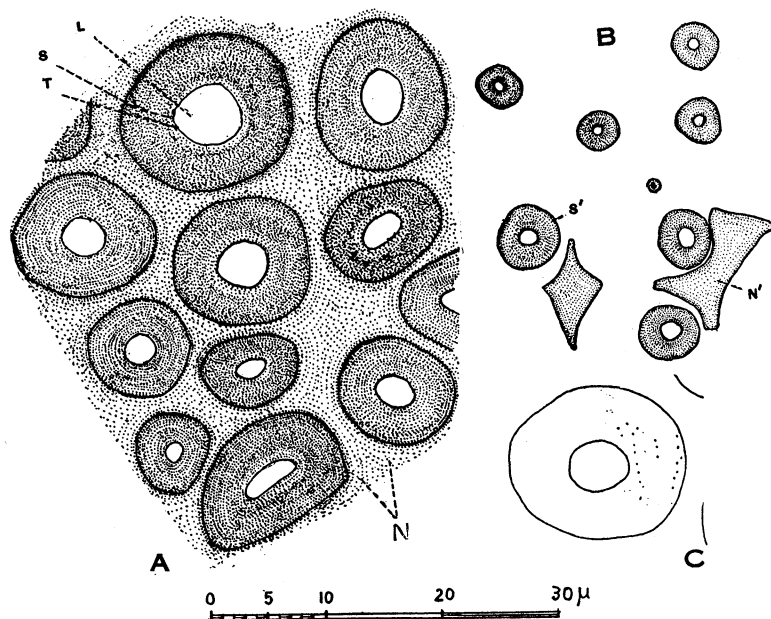


FIG. 1. *A* and *B*, cross-section of xylem of *Tecoma* sp. *A*, before treatment; *B*, after desilicification and drying—*L*, lumen; *S*, secondary thickening; *T*, tertiary thickening; *N*, middle lamella and primary thickening. *C*, secondary thickening of a single tracheid, showing a number of skeleton rods.

* Lapachol is a natural quinone dye, which is found in vessels of the heart-wood of several species of *Tecoma*, natives mainly of South America. It forms a sulphur-yellow dust over the cut surface of the wood and, when moistened by ammonia or dilute sodium carbonate, turns deep wine-red, serving as a reliable character in the identification of the wood. Also, fine chips of the wood, upon standing in a test tube partly filled with dilute aqueous solution of sodium carbonate, will turn the liquid a deep red color.

easily differentiated from each other. In the xylem of *Tecoma* and many other genera, these two membranes differ little from one another in appearance. They stain nearly alike, have nearly the same index of refraction, and are similar in chemical and physical composition, so that, without special technique, they are indistinguishable from one another (as shown in *N*, FIG. 1). They may be differentiated, however, in certain refractive media, as shown by the writer in an earlier paper;* or, better, by mounting cross-sections 10–20 μ thick in dilute Shultze's solution, warming the slide slightly, and observing under high power. In Schultze's solution the true middle lamella is dissolved before the primary thickening of the fiber. These two membranes together compose about one half of the cross-section area, and, when treated with phloroglucinol and hydrochloric acid, give the deep red reaction for furfural. It is also a noteworthy fact that the index of refraction of these layers, which is about 1.59 (that of the middle lamella being slightly higher than that of the primary thickening), approaches the refractive index of the calcified wall of the calcareous alga *Penicillus* ($n = 1.60$). *Tecoma* forms an unusually good subject for study because there are few genera in which the primary thickening is as well developed as in this genus. In many genera, even those in which the secondary layer is well developed, as in *Quercus*, *Caesarea*, or *Aspidosperma*, the primary thickening is extremely thin and may even appear to be absent.

2. SECONDARY AND TERTIARY THICKENINGS

The secondary thickening (*S*, FIG. 1) is well developed in all the lapachol-yielding species of *Tecoma*, and appears more or less rounded or even circular in outline in the transverse section. The index of refraction of this thickening of the fiber is slightly below that of quartz, the refractive index of which is 1.54. A thin highly refractive tertiary layer (*T*) borders the lumen (*L*). Neither of these thickenings reacts for furfural, and both are therefore unlignified in all the lapachol species of *Tecoma* examined. In other genera the thickening is commonly lignified.

When cross-sections are first mounted in glycerine or water, the secondary layer appears to be of homogeneous composition;

* Brown, F. B. H. The refraction of light in plant tissues. Bull. Torrey Club 47: 243–260. f. 1–4. 1920.

but, upon standing a few hours, small isolated areas (FIG. 1, *C*) may be distinguished. These areas appear to be slightly more refractive than the material of which the rest of the secondary thickening is composed, when the wall has taken up as much as it will of the liquid in which it is mounted. They are circular in outline, 1–3 μ in diameter, approximately two hundred in number in the cylindrical portion of the fiber, and distributed quite evenly through the secondary thickening of the wall. They are without order of arrangement except that those of larger diameter appear to be placed near the outside. The exact size and position in the fiber wall of areas seen with sufficient clearness to be drawn with the Abbé camera are shown in FIG. 1, *C*; numerous others could be seen distributed evenly through this membrane but not with sufficient clearness to be projected.

One effect of imbibition upon the membrane-mass would be to lower the index of refraction of that portion which takes up the liquid. From the fact that the relatively more refractive areas appear in the membrane after the imbibition of water or glycerine, it is indicated that these portions of the membrane imbibe little or no liquid; the remainder of the membrane, on the other hand, is evidently composed of hygroscopic material. The impermeable areas, in all probability, represent the cut ends of silicious rods which, as will be shown presently, form a skeleton-like structure in the secondary thickening of the fiber.

3. HISTOLOGICAL ELEMENTS OF THE SECONDARY THICKENING

The secondary thickening of fibers of the xylem of *Quercus*, *Hicoria*, *Caesarea*, *Aspidosperma*, and the majority of woody plants forms nearly the entire cell-wall. It is without doubt essential to the mechanical strength of these sclerous membranes and is never absent in fibers the longitudinal dimensions of which tend to remain unchanged under different conditions of moisture.

As previously mentioned, small isolated portions of this thickening of the fiber in *Tecoma* are composed of non-hygroscopic material. If the untreated section is placed upon a mica slip and held over an alcohol flame until the fibers are partly burned to ash, numerous hyaline, non-combustible, rods of mineral composition are left partly free along the burned margin of the secon-

dary layer, held in position by what remains of the charred matrix (FIG. 2, *A*). In all probability the cut ends of these mineralized rods are identical with the small non-hygrosopic areas which were observed in the untreated membrane after being mounted for some time in water or glycerine. The material of which these tracts in the wall are composed is therefore non-hygrosopic as well as non-combustible. The solubility of the rods so isolated was tested in various reagents; but such results can have little significance as to the original composition, since the chemical composition, as well as the refractive properties of the rods, was found to undergo great change during the process of burning. In some cases, the rods became covered with a thin film of black material highly resistant to nitric, sulphuric, hydrochloric and even hydrofluoric acid.

As will be shown presently, these rods are composed, in part at least, of silicious material and form a skeleton-like structure in the secondary thickening of the fiber wall. The remainder of the secondary thickening (in which the rods are imbedded) may be termed the colloidal matrix, for reasons which will be given more fully later.

The histology of the secondary thickening of the fibers or tracheids in the wood and of the fibers of the bast in all species examined by the writer is essentially the same as that observed in the xylem of *Tecoma*. It is composed of the following two structural elements, which differ from each other in their physical and mechanical properties as well as in their chemical composition: namely, (1) a non-hygrosopic silicious skeleton imbedded in (2) a hygrosopic colloidal matrix. With little doubt,

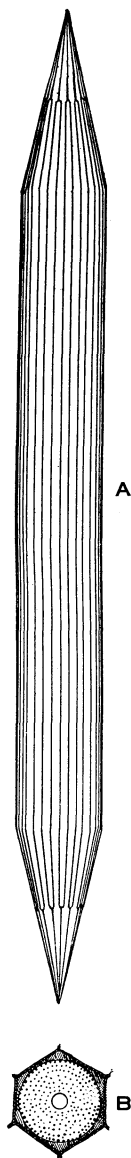


FIG. 2. Silicious skeleton, diagrammatic. *A*, longitudinal view; *B*, transverse view, the shaded portion representing middle lamella and primary thickening.

these structures are independent of each other in the properties which they impart to the wood. They may therefore be separately considered.

a. Silicious skeleton

Structure.—The longitudinal rods, of which the silicious skeleton of tracheids and fibers is composed, are nearly straight, parallel, and extend longitudinally in the colloidal matrix from one end of the tracheid or fiber to the other.

The number of vertical rods in a skeleton varies according to the genus or species, from possibly as few as four in the tracheids of *Trochodendron* to possibly as many as two hundred in the fibers of *Tecoma*.

These rods occasionally branch or coalesce—more frequently in some species than in others. The coalescence probably serves to reduce the number of vertical rods in the tapering ends of a fiber or tracheid, as shown diagrammatically in FIG. 2; in conifers the rods branch around the large circular pits or become reticulate where the pits are numerous; in *Pinus Strobus*, a silicious ring encloses the extreme border of each large pit. Scalariform pitting in particular makes necessary a great reduction in the number of vertical rods in a tracheid. Thus in *Trochodendron* a single rod of comparatively large diameter passes to each side of a vertical series of the transversely elongated pits and a transverse rod of smaller diameter passes between each two pits of the series and joins at either end to each of the vertical rods like the rounds of a ladder. Hence, judging from the structure of the skeleton, the pits and pit-areas would not swell or shrink in either the longitudinal or the transverse planes. The rods are filamentous in shape and are, as before mentioned, probably less than $3\ \mu$ in diameter. The details of structure, as summarized above, may be observed in burned preparations, as follows: from small transverse sections of the xylem of *Tecoma* 15–20 μ thick, it is found that as many as twenty rods may be seen partly exposed along the burned outer margin of the secondary layer (FIG. 3, A). On burning deeper inward toward the center of the fiber, other rods would undoubtedly be exposed; hence it may be assumed that not less than a hundred rods may be present in the fiber, of which only twenty are exposed at the margin. In unburned

sections mounted in glycerine, the number of rods as estimated from the refractive areas was placed at about two hundred. The difference in estimates from burned and unburned material

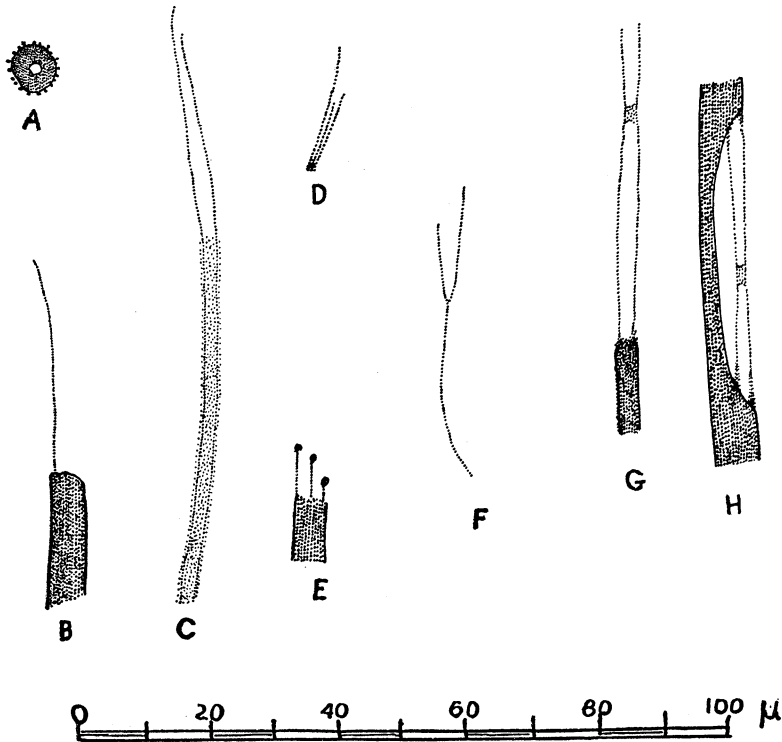


FIG. 3. Burned material. A, cross-section of fiber showing exposed skeleton rods; B, C, D, G, H, showing unbranched rods; G and H, showing lateral ties; F, branched rod; E, glass beads formed by heat.

may be explained from the probability that part of the rods in the burned material may have been broken off close to the matrix and therefore were not seen. The number of rods in a fiber of *Tecoma* may therefore be estimated at not less than one hundred and possibly twice that number.

The relative position of the rods in a fiber and the manner of branching may be observed from burned macerated material. When the wood of *Tecoma* is treated with Schultze's solution, using 50 per cent nitric acid, it is possible to dissolve away both the middle lamella and primary wall of the fiber. The tertiary

layer in most of the fibers is thin and poorly defined, hence what remains of the fiber wall after thorough maceration is composed almost wholly of secondary thickening. When these macerated fibers are washed, dried, then burned on a mica slip, the isolated or partly isolated rods, and their relative position and branching may be observed. In *B*, FIG. 3, is seen an isolated unbranched rod over $30\ \mu$ in length, projecting from the charred end of a partly burned fiber; in *D* are shown three such rods. Two parallel unbranched rods (FIG. 3, *C*) were traced a distance of $90\ \mu$, partly free and partly imbedded in a transparent matrix of unburned material, as shown in the drawing. In burned tracheids of *Trochodendron*, unbranched rods 1.15 mm. in length were found in one instance. Occasionally the rods branch as shown in *F*, from *Tecoma*. The diameter cannot be accurately determined from burned material, since products of combustion and fusion adhere as a film to the outer surface of the rods. It is probable that the lateral ties observed between neighboring rods, as shown in *G* and *H*, FIG. 3, are merely the products of combustion and hence not a structural feature of the skeleton. From such data the structure of the skeleton, as well as its position in the fiber wall, may be inferred. The essential feature of the skeleton consists in the presence of longitudinal rods, and these were never found absent from the fibers and tracheids of the wood or in the fibers of the bast in any species examined by the writer. Other details of the skeleton, however, may vary considerably, according to the species, genus, or family in which it occurs. Thus, in the thin-walled fibers of *Ochroma lagopus*, the rods are few in number; in the thick-walled fibers of *Tecoma*, *Aspidosperma*, *Caesarea*, *Cedrela*, *Swietenia* and *Hicoria*, they are numerous; in *Guaiacum*, they are numerous and of extremely small diameter; in *Pinus Strobus*, they are relatively much branched; in *Araucaria brasiliana*, they are few and of unequal diameter. Silicious rods are present in the fibrous strands in the haulms of *Secale cereale*, but in the walls of the epidermis the silica is distributed more uniformly, so that, after burning, the cellular structure including the guard cells of the stomata is preserved.

Chemical composition.—The skeleton-rods in all species examined were found to be composed, in large part at least, of non-

combustible material. That the chemical composition varies in different species is certain, but silica or some silicate is evidently present in every case. That the skeleton-rods of *Tecoma* are highly silicified is plainly shown from an examination of burned macerated fibers before and after treatment with hydrochloric, nitric, and hydrofluoric acid. Before treatment with acid the rods are invariably present; also, after treatment with hydrochloric or nitric acid they are present; but after treatment with hydrofluoric acid they are invariably absent.

Furthermore, it is of great interest to note that the heat generated by an alcohol flame, together with that of the burning fiber, is sufficient to cause the formation of glass beads, usually at the ends of the silicious rods, as shown in FIG. 3, *E*. This often happens when the calcium-rich fibers of *Tecoma* are burned and less frequently in calcium-poor material like *Secale*. These beads are insoluble in hydrochloric, nitric, or sulphuric acid and have an index of refraction of 1.59, approaching that of flint glass. The calcium is, in all probability, changed to lime by the heat, and would thus act as a flux upon any silica in the rods, causing the formation of the highly refractive glass beads. The result would be the same whether the rods were composed of silica, such as quartz or opal, or of highly silicified material. Also, the same reaction to hydrofluoric acid would be obtained in either case, since either silica or silicates would be quickly dissolved by this reagent.

The question now arises whether the silica in the secondary thickening of the *Tecoma* fiber is actually present in an amount that would be necessary, if it is assumed that the skeleton rods are composed either of silica or of highly silicified material. Macerated material may be used in an approximate analysis of the mineral content of this portion of the fiber wall, since in the species of *Tecoma* examined the vessels, ray cells, and elements other than the fibers have thin walls and do not make up a material part of a macerated preparation. It was thus possible to obtain several grams of material made up in large part of the secondary thickening of fibers; after combustion, 1.8 per cent (of the dry weight of the fiber) of mineral matter was obtained and .1 per cent (of the dry weight of the fiber) of silica or silicic acid. Silicon

is therefore not abundant in the secondary thickening of the fiber of *Tecoma*, but if concentrated in the skeleton rods the amount would be more than sufficient to form a skeleton with two hundred vertical rods composed either of silica or of some highly silicified material.

Various evidences make it almost certain that the composition of the rods varies in different families, genera, and species, though silica or silicious matter may always be present. This is indicated in the fact that the effect of hydrofluoric acid upon the mechanical rigidity of the fiber is quite different in some species from what it is in others. Thus in *Tecoma* and several other genera, as will be described more fully presently, the fibrous tissues of the xylem suddenly contract more than 20 per cent in length during treatment with hydrofluoric acid; the wood of *Aspidosperma* and of numerous other genera, on the other hand, is merely softened by this treatment. Also, hydrochloric acid attacks the skeleton rods of *Guaiacum* sp. and softens the wood sufficiently to permisectioning in the microtome; but with this acid there is no material contraction of the fibers, and the skeleton rods are still present in the ash, though a large portion of the outer mineralized film has apparently been dissolved by the acid. In this case the rods may be composed of a central axis of silica or of highly silicified material, enclosed by a thin outer covering of mineral composition which is partly soluble in hydrochloric acid.

That the skeleton rods are not composed entirely of crystalline silica is evident from the fact that when the macerated fibers of *Tecoma*, *Aspidosperma*, *Secale* and all the other genera examined are mounted in strong sulphuric acid, the entire wall is dissolved without leaving any insoluble remains which might be positively identified as part of a skeleton rod. But the rods seem to be more slowly disintegrated than the matrix, and hence they not infrequently remain visible a short time in the acid after the rest of the wall has been dissolved. The evidences as a whole therefore favor the conclusion that the skeleton rods are composed of highly silicified material, the composition of which varies in the different families, genera, and species.

Physical properties.—As before mentioned, the rods probably imbibe little or no liquid and hence under ordinary temperature

conditions would tend to remain of constant length, though the water content of the matrix might vary considerably. With the application of force, however, the rods would shorten or lengthen within the elastic limits of the material of which they are composed. Under high temperatures the rods appear to undergo change in composition, possibly giving off moisture, and may then be observed to contract in length.

b. Colloidal matrix

The material in which the skeleton rods are imbedded exhibits essentially the properties of matter in the colloidal state. Besides being highly hygroscopic and gelatin-like in many of its microscopic characters, it has the property of imbibing methylene blue and other colloidal solutions even in the living condition. The term colloidal matrix is therefore used to designate that portion of the secondary thickening of fibers and tracheids in which the silicious skeleton is imbedded; it is apparently stretched upon the silicious skeleton under longitudinal tension strain. This is indicated from the fact that after a macerated fiber of *Tecoma* (A, FIG. 4) has remained a few minutes in hydrofluoric acid, it suddenly contracts 36 per cent or more longitudinally, and, at the same time, increases often as much as 100 per cent in diameter, as shown in B, FIG. 4,

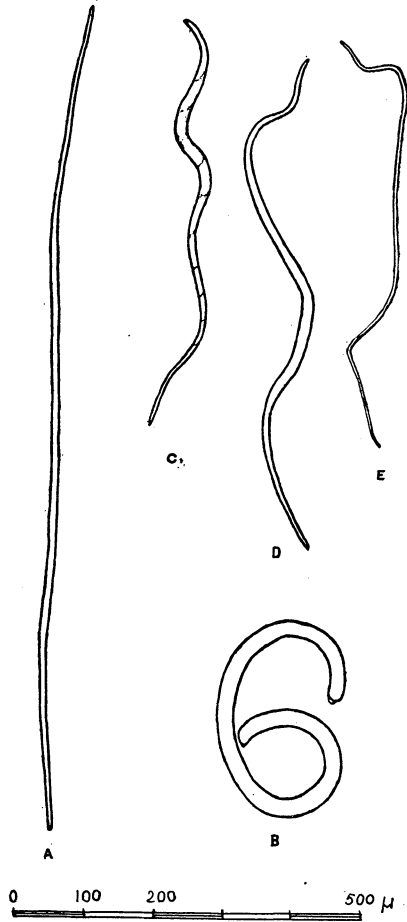


FIG. 4. Isolated fibers of *Tecoma*. A, before treatment; B, same fiber after desilicification; C, D, typical desilicified fibers; C, showing spirals; E, same as D after drying.

which is an accurate drawing of *A* after desilicification. Usually the contracting fibers increase much more in diameter toward the center than near the ends, as has been accurately shown in *C* and *D*. In any case the secondary thickening of the fibers contracts in length and expands in diameter with an elastic force sufficient to separate this thickening from the primary thickening, and to burst the middle lamella, medullary rays and other parts of the woody tissue sufficiently to allow the transverse expansion.

After the dissolution of the silicious skeleton the colloid matrix is gelatin-like in texture, without mechanical rigidity, and assumes various curved outlines as shown in *B*, *C*, and *D*. It absorbs water freely, and, when dried, shrinks greatly in both diameter and length as shown in *E*, FIG. 4, which is an accurate drawing of *D* after drying. The contraction in diameter is more accurately shown in FIG. 1, *B*, which represents the remains of *A* after desilicification and drying. The primary thickening and middle lamella (*n*) are broken into fragments but shrink comparatively little (*n'*).

The structure of the colloidal matrix may be observed in desilicified fibers mounted in water. Owing to differences in refraction, delicate spiral lines of material may be observed in the body of the matrix as shown in FIG. 4, *C*. Further evidence of the spiral structure of the colloidal matrix is found in the inclination of the slit-like orifices of the fiber pits, which coincides with that of the spirals.

III. INHIBITING EFFECT OF SKELETON UPON THE SWELLING OF THE MATRIX

Since the non-hygroscopic skeleton rods would remain constant in length with the varying moisture content of the matrix, they would inhibit any tendency of the matrix to swell or shrink longitudinally, except in so far as would be permitted by their elasticity. With the application of force, a certain amount of longitudinal compression or stretching of the skeleton rods would undoubtedly be permitted; hence the slight longitudinal swelling and shrinking of woody tissues, which at most amounts to only 1 to 2 per cent, may take place by reason of the elastic property of the rods.

Any tendency of the matrix to shrink or swell along the diameter of the fiber, would not be inhibited by the unbranched vertical rods, since these would move apart or approach with the swelling or shrinking of the matrix. As previously explained, the branching of the skeleton in pit areas would indicate that these areas of the wall swell or shrink only in thickness if at all.

IV. EFFECT OF DESILICIFICATION UPON THE MECHANICAL RIGIDITY OF THE TISSUES

That the silicious skeleton is of fundamental importance to the mechanical rigidity of the tissues is indicated by the effect of desilicification. The haulms of *Secale*, for example, when placed in hydrofluoric acid, contract with elastic force over 30 per cent in length and at the same time expand approximately 100 per cent in diameter. The desilicified tissues have a rubber-like elasticity and may be stretched nearly to the original length.

Remarkably similar effects are obtained when the xylem of *Tecoma* is desilicified. In the accompanying table (TABLE I), the length of a block of wood and the radial and tangential dimension are recorded at indicated intervals during treatment; the gain or loss relative to the respective dimensions of the tissue in the dry state are incased in parentheses.

The rate and relative amount of swelling or contraction in length and in the radial and tangential dimensions of the block, the measurements of which are given in the table during the period of treatment are shown in the graph, FIG. 5. During the five and one half hours in boiling water (*A* to *B*), the tissues swelled barely 1 per cent in length, though both diameters increased more than 10 per cent. At length, all dimensions became stable in water and changed but slightly if at all during the first seventeen hours (*B* to *B'*), when the water-saturated wood was transferred to strong hydrofluoric acid.

Up to time *B'*, only the usual phenomena of swelling in woody tissues are recorded, of which the relative constancy of length is the remarkable but characteristic feature. At *B'*, however, changes of an essentially different character began; the length, which up to this time had remained almost constant, now rapidly contracted over 20 per cent, while the radial and tangential diameters expanded over 40 and over 50 per cent, respectively.

TABLE I

CHANGES IN LENGTH AND DIAMETERS OF XYLEM OF *Tecoma* UNDER DIFFERENT CONDITIONS.

In parentheses is indicated the per cent of gain or loss, relative to dimensions in the dry state.

Length	Radial diameter	Tangential diameter	Hours	Conditions
5.52 mm.	8.53 mm.	8.47 mm.	10.	In air, 100° C.
5.52 "	9.07 " (+6)	9.09 " (+7)	10.5	In water, 100° C.
5.53 " (+0.1)	9.40 " (+10)	9.50 " (+11)	11.0	" " "
5.53 "	9.48 " (+11)	9.55 " (+12.7)	11.5	" " "
5.53 "	9.48 " "	9.55 " "	13.0	" " "
5.53 "	9.48 " "	9.60 " (+13.)	15.0	In HF
5.53 "	9.48 " "	9.80 " (+15.)	19.0	" "
5.53 "	9.48 " "	9.80 " "	22.0	" "
5.53 "	9.48 " "	9.80 " "	32.0	" "
4.7 " (-14.8)	11.3 " (+32)	14.22 " (+67.8)	33.5	" "
4.5 " (-18.0)	12.2 " (+43)	15.7 " (+85)	35.0	" "
4.4 " (-20.3)	11.0 " (+29)	14.5 " (+71)	38.0	" "
4.3 " (-22.0)	11.0 " "	13.3 " (+57)	43.0	" "
4.3 "	11.0 " "	13.3 " "	48.0	" water
4.3 "	11.0 " "	13.3 " "	56.0	" "
3.3 " (-40.0)	6.9 " (-19)	7.3 " (-13.8)	56.5	" air, 100° C.
3.3 "	6.9 " "	7.3 " "	6.4	" " "

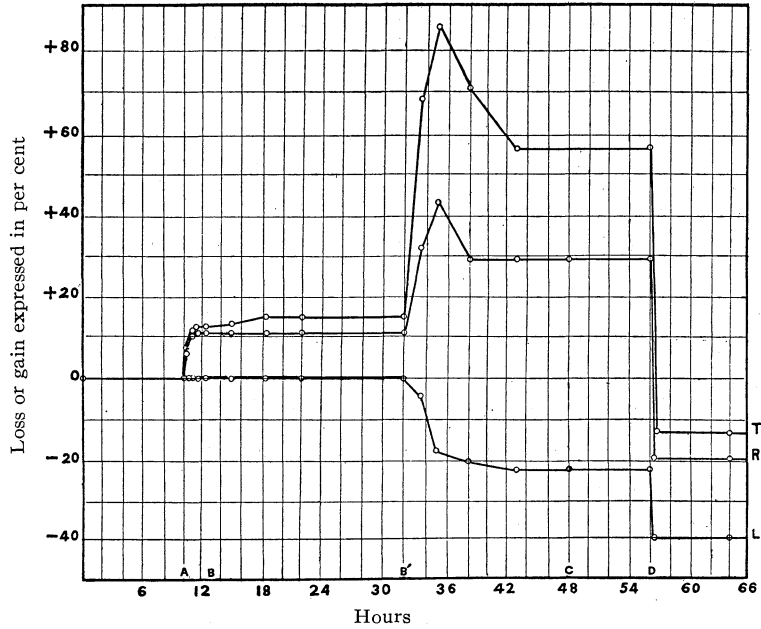


FIG. 5. Graph showing changes in the different dimensions of the xylem of *Tecoma* during treatment; A—B, in boiling water; B—C, in hydrofluoric acid. A collapse of mechanical rigidity commences at time, B', C—D, in running water; D, in air, 100° C.

The transverse dimensions subsequently contracted to some extent, but after a few hours all dimensions remained nearly constant, whether left in acid, or transferred to water (*C* to *D*). The subsequent great contraction (*D*) of all dimensions which took place when the desilicified tissues were dried, indicates the almost complete loss of mechanical rigidity of the xylem after desilicification.

The changes which occur in the longitudinal dimensions of a block of the xylem of *Tecoma* during treatment are essentially the same as those which occur in the isolated fiber under the same treatment. Probably up to time *B'* the skeleton rods had not been weakened by the acid. But immediately after *B'* there was a rapid contraction in length and expansion in the transverse dimensions, such as would occur with the collapse of the skeletons; the entire course of the curves during the first part of the time, *B' C*, indicate the collapse of the mechanical element of the xylem.

A similar amount of longitudinal contraction and transverse expansion occurred in the xylem of all of the thirty lapachol-yielding samples of *Tecoma* examined. Similar changes were observed in approximately one-fifth of the species of the other genera and families examined by the writer; but the amount varied with the genus and species. Many species such as *Aspidospermas*, showed little or no longitudinal contraction during desilicification. Such differences in the effect of desilicification are reasonably explained on the assumption that the rods must differ in chemical composition, according to the species, although silicious material may be present in each case.

V. SUMMARY

The longitudinal dimensions of the xylem and bast in either living or dead tissues are subject to little variation upon soaking in water or drying, by reason of a silicious skeleton in the secondary thickening of the fibers and tracheids. This skeleton is composed of sparingly branched non-hygroscopic rods of silicified material which extend longitudinally in the hygroscopic cell-membrane from one end of the fiber or tracheid to the other.

Except for local areas, the longitudinal skeleton rods are not branched or united in a way to prevent them from being spread

apart or crowded together; hence the swelling and shrinking of the cell-wall may take place at right angles to the axis of growth.

In the vicinity of pits, such as the circular pits of *Pinus Strobus* or the scalariform pits of *Trachodendron*, the vertical system of rods is replaced by reticulate branches or transverse connections which would probably inhibit swelling or shrinking of these areas in all directions except, possibly, in thickness.

The skeleton rods are composed of highly mineralized material, the composition of which varies in the different families, genera, and species; but silica or some silicate is present in at least a large number of cases.